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BREEDING BIOLOGY OF ACADIAN FLYCATCHERS IN A BOTTOMLAND HARDWOOD FOREST

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ABSTRACT.—From 1993–1995, we located and monitored 601 Acadian Flycatcher (*Empidonax virescens*) nests in a large contiguous tract of bottomland hardwood forest on the White River National Wildlife Refuge, Arkansas. Annual reproductive success was significantly different among years; ranging from 10–25% (Mayfield estimate) over the three years of the study. There was no significant difference in nest success among study plots, with nesting success showing a trend of increasing late in the breeding season. Clutch size for nonparasitized nests averaged 2.9 ± 0.02 (SE) eggs with a mode of 3. Rates of Brown-headed Cowbird (*Molothrus ater*) parasitism were low (21%), accounting for 7% of all nest failures. However, parasitism by cowbirds resulted in a reduction of clutch size for nests initiated early (i.e., first nests and replacements) in the breeding season. Predation was the leading cause of nest failures, accounting for 75% of all failures. Snakes and avian predators were thought to be the leading cause of nest failures. Although additional factors must be investigated, preliminary results indicate that nest predation is a major influence on this population, despite the size of the forest tract. *Received 10 June 1997; accepted 27 Oct. 1997.*

Recent trends of many forest interior songbird populations have raised questions concerning the stability of these populations (Robbins et al. 1989, Askins et al. 1990, Terborgh 1992). As a result of the high degree of forest fragmentation and habitat loss in the eastern United States, factors on the breeding grounds have been suggested as the primary cause of migrant declines, presumably through decreased reproductive success (Martin 1992; Robinson et al. 1995a, b). In the southeastern United States, land conversion to agriculture and construction of levees have eliminated bottomland hardwood forest from much of the Mississippi Alluvial Valley (MAV; Pashley and Barrow 1992), which presumably has contributed to the decline of many forest interior songbird populations.

In this study, we initiated a demographic investigation of Acadian Flycatchers (*Empidonax virescens*) in an unfragmented bottomland hardwood forest in eastern Arkansas. The breeding biology of this species has been poorly documented, with the only detailed studies occurring on the northern periphery of its range (see Mumford 1964, Walkinshaw 1966). Here, we present an analysis of the breeding biology of Acadian Flycatchers in a large contiguous tract of bottomland hardwood forest in the Lower Mississippi Alluvial Valley. We also assess some of the factors likely to affect reproductive success.

STUDY AREA AND METHODS

Study area.—White River National Wildlife Refuge (NWR) is located in Phillips, Desha, Monroe, and Arkansas counties in eastern Arkansas, and appears as a long, narrow physiographic island in a highly fragmented landscape. Situated within the flood plain of the White River approximately 4–5 km above its confluence with the Mississippi River, the refuge consists almost entirely of bottomland hardwood forest. The 60,000 ha area is 4.8–16 km wide and extends approximately 104 river km along the White River. Of the total refuge acreage, 90% is forested, 9% is in waterways and lakes and 1% is in agriculture [U.S. Fish and Wildlife Service (USFWS) 1980].

Topography on the refuge is typical of naturally flooded bottomland forest, with wide flats broken by low ridges and swales. Bayous, oxbow-lakes, and sloughs are common throughout the refuge. Elevations range from 41–51 m above Mean Sea Level with 98% of the area falling below the 48-m contour (USFWS 1980). Flooding from the headwaters of the White River and backwaters of the Mississippi River annually inundates much of the refuge under the 45.7-m contour (J. Denman, pers. comm.). Except for the small acreage of upland hardwoods, the refuge is classified as palustrine, forested wetlands (Cowardin et al. 1979).

For this study, six rectangular 50-ha (500 m × 1000 m) plots were established within a single 1376 ha management compartment (Number 8) of contiguous homogenous habitat. The dominant overstory tree species on these plots were overcup oak (*Quercus lyrata*), Nuttall oak (*Quercus nuttallii*), green ash (*Fraxinus penn-*

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sylvanica), bitter pecan (*Carya aquatica*), American elm (*Ulmus americana*), cedar elm (*Ulmus crassifolia*), waterlocust (*Gleditsia aquatica*), sugarberry (*Celtis laevigata*), and cypress (*Taxodium distichum*). Understory vegetation was primarily seedlings and saplings of canopy trees (i.e., *Quercus* regeneration), plus possumhaw (*Ilex decidua*), swamp privet (*Forestiera acuminata*), hawthorn (*Crataegus* spp.), and water elm (*Planera aquatica*). For additional information on the study area see Wilson (1997).

Nest monitoring.—Intensive nest searches were conducted on each plot throughout the breeding seasons of 1993–1995 to locate as many Acadian Flycatcher nests as possible (no plots were delineated in 1993 and nests were only located and monitored during June of 1993). Once a nest was located, its contents were noted. Poles with convex mirrors attached to one end were used to examine nests when contents could not be ascertained from the ground (Parker 1972). If nest height was too great for use of mirror poles (ca 8 m), the nest was observed from a distance using binoculars. Contents or stage of nesting was then determined by the behavior of adult birds (e.g., frequent visits by adults carrying food indicated the nest contained nestlings). Nest locations were then measured to the nearest grid point using a compass and a SONIN Combo Pro electronic distance estimator and recorded on a grid map to facilitate relocation. Nests were revisited every 3–4 days following Breeding Bird Inventory and Research Database (BBIRD) protocol (Martin et al. 1996) to determine the fate of each nest as accurately as possible.

Clutch size was based on the number of Acadian Flycatcher eggs over all nest checks. Nests that contained Brown-headed Cowbird (*Molothrus ater*) eggs may bias estimates of mean clutch size because it is possible that cowbirds removed eggs before the nest was found. Thus, estimates of clutch size are minimum estimates. Likewise, cowbird eggs and nestlings may disappear before nests are found, resulting in minimum estimates of brood parasitism.

Nesting success.—Nesting success was calculated by the methods of Mayfield (1961, 1975; see also Hensler and Nichols 1981), which estimate the probability of nest survival based on nest exposure days. A daily probability of nest survival (D) was calculated for each stage of the nesting period [i.e., egg stage (from first egg to first hatching) and the nestling stage (hatching to fledging)]. Nest-stage survival estimates (S) were obtained using the equation: $S = D^X$, where X is the number of days in the nest-stage. For Acadian Flycatchers, the egg stage was 15 days and the nestling stage was 14 days (see Results). Estimates of overall nesting success were obtained in the same manner. That is, the overall daily probability of nest survival was raised to the power of 29 (i.e., number of days in nesting period) to estimate the probability of nest survival (Hensler and Nichols 1981). Nests were excluded from analysis for any of three reasons: (1) the nest failed prior to laying of the first egg; (2) observers caused or influenced mortalities; and (3) the nest outcome was unknown. A nest was considered successful if it fledged at least 1 Acadian Flycatcher young. Conversely, a nest was considered a failure if its entire contents disappeared between checks and if insufficient time expired between checks for young to fledge, or if the only young to fledge were not Acadian Flycatchers.

Statistical analysis.—Tests of hypotheses comparing mean estimates of nest survival were conducted using the computer program CONTRAST (Hines and Sauer 1989, Sauer and Williams 1989) in the Microsoft-DOS operating system. Student's *t*-test and Analysis of Variance (ANOVA) were used to test for univariate differences in group means using PC-SAS (Vers. 6.11, SAS Institute 1992).

RESULTS

Nesting stages.—Females began building nests approximately 5–10 days after arrival with the majority of first nests constructed between 11 May and 22 May. Analysis of initial egg laying dates followed a bimodal distribution (Fig. 1), suggesting that Acadian Flycatchers produce more than one brood in the southern portion of their range. First eggs were laid on 19 May 1994 and 17 May 1995. One egg was laid per day, and incubation started with the penultimate egg. The mean incubation period was 14.3 days (standard error = 0.13, $n = 73$), and the mean nestling period was 13.6 ± 0.10 days ($n = 58$). Clutch size for all nonparasitized nests reaching the incubation period was 2.9 ± 0.02 eggs ($n = 213$; range = 2–4; mode = 3).

Parasitism and clutch size.—Brood-parasitism by Brown-headed Cowbirds averaged 21% during the study with only 8% of parasitized nests containing more than one cowbird egg (Table 1). However, brood-parasitism influenced clutch size of Acadian Flycatchers ($t = 4.27$, 100 df, $P < 0.001$) for all years combined. Parasitism had no significant effect on clutch size in 1993 ($t = 0.481$, 16 df, $P > 0.05$) and 1994 ($t = 0.545$, 60 df, $P > 0.05$), but clutch size was significantly lower in parasitized nests in 1995 ($t = 4.56$, 73 df, $P < 0.001$). Analysis of early and late nests (those initiated before or after 14 June; see Fig. 2) for all years showed that late-season nonparasitized clutches were significantly lower than early-season nonparasitized clutches ($t = 2.29$, 84 df, $P < 0.02$) and parasitized clutches were significantly lower than nonparasitized clutches during the early season ($t = 5.05$, 77 df, $P < 0.001$). Results of two-way ANOVA yielded a significant interaction between

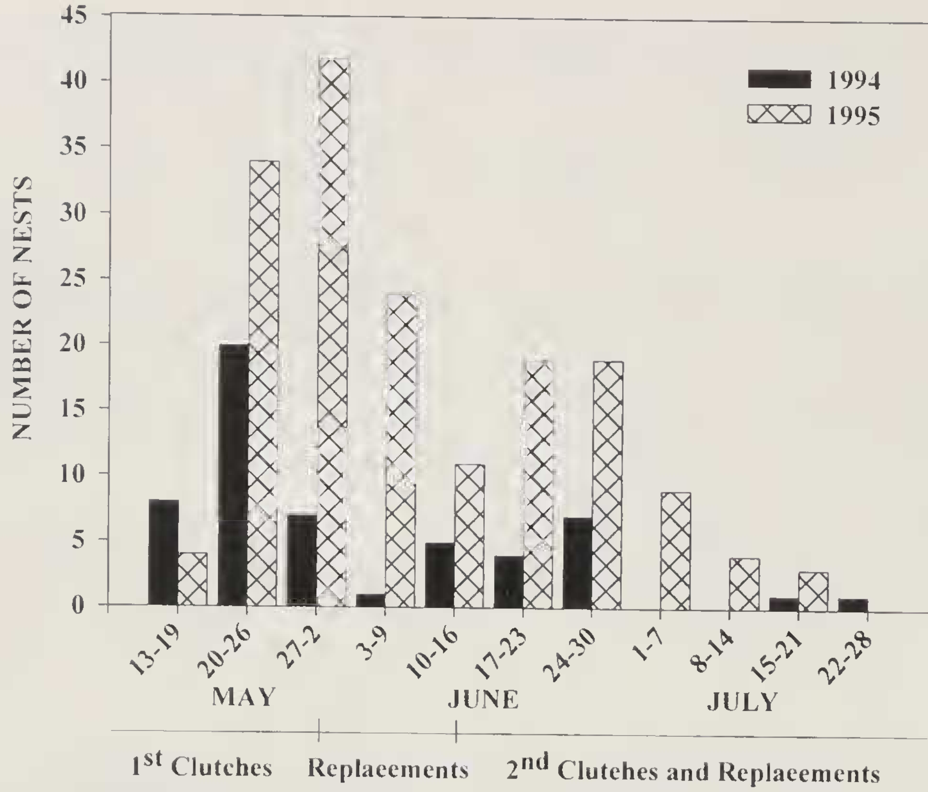

FIG. 1. Frequency distribution of initial egg laying dates for Acadian Flycatchers on White River NWR, 1994–1995.

clutch size of parasitized and nonparasitized nests across the breeding season [(i.e., first clutches, replacement clutches, and second clutches) $F = 8.01$, df = 5, 279, $P < 0.001$; Fig. 2].

Nesting success.—Acadian Flycatcher nesting success (probability of surviving the 29-day nesting period) on White River NWR varied throughout the study, ranging from 0.10 to 0.25 across all years of the study (Mayfield estimate, Table 2). Annual daily survival rates differed among years ($\chi^2 = 6.63$, 2 df, $P = 0.03$) with daily survival rates being significantly lower in 1993 ($\chi^2 = 4.11$, 1 df, $P = 0.04$). Daily survival rates for egg stage versus nestling stage were analyzed separately by plots within a year, among years and pooled over all years. No significant difference between egg stage and nestling stage rates of survival was found when the α-level was corrected using a Bonferroni adjustment ($\alpha = 0.008$; Rice 1989). Analysis of early and late nests showed a significant difference in 1994 with late nests having a higher probability of survival than early nests ($\chi^2 = 5.50$, 1 df, $P < 0.02$; Table 2). No significant differences were found between early and late nests in 1995 and because all nests in 1993 were considered early nests, no analysis was performed.

Nest failures were analyzed according to the causes of nest failure and the stage of nesting when failure occurred. The primary cause of nest failures in all years was predation, accounting for 75% of all failures (Table 3). Nest failure attributed to Brown-headed Cowbird parasitism was variable but low in all years, comprising 7% of all nest failures. Failures attributed to parasitism included nests that fledged at least one cowbird young, but no conspecific young, as well as nests that were abandoned after parasitism or the effects of parasitism [i.e., removal of host egg(s)]. Failures in which the entire contents of the nest disappeared between checks accounted

TABLE 1. Rates of Brown-headed Cowbird parasitism on Acadian Flycatchers, White River NWR, 1993–1995.

Year	Parasitism rates[a]	# Eggs[b] 1	2
1993	13.5 (74)	12.2	1.3
1994	20.2 (129)	17.8	2.3
1995	22.6 (300)	21.3	1.3
1993–1995	20.7 (503)	19.1	1.6

[a] Percentage of Acadian Flycatcher nests parasitized (sample size).
[b] Percentage of total nests.

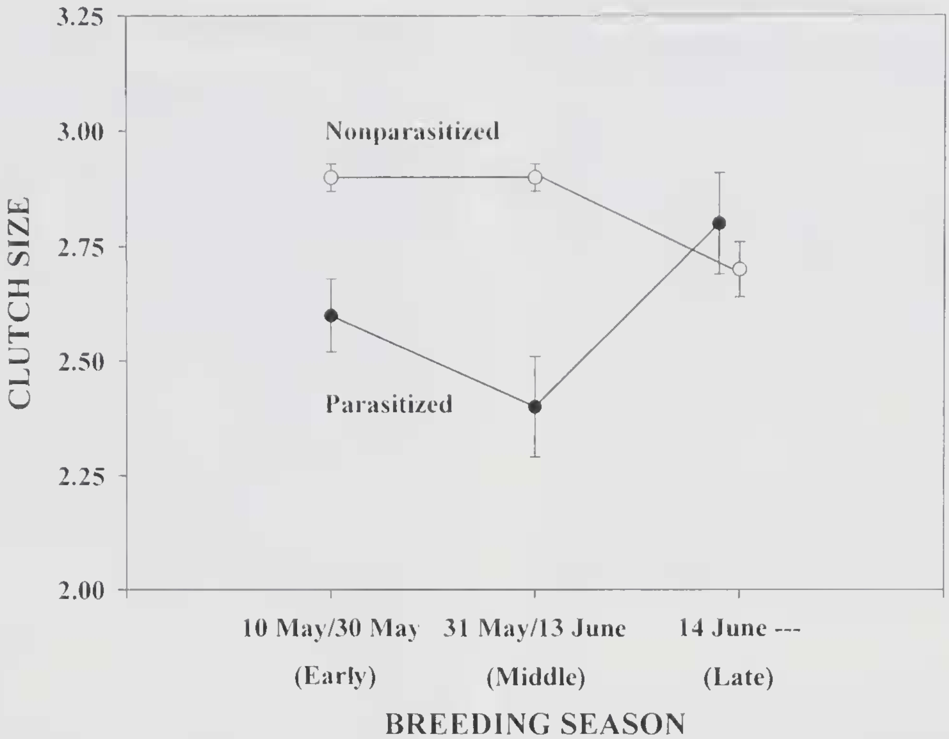

FIG. 2. Clutch size for parasitized and nonparasitized Acadian Flycatcher nests in three time periods within the breeding season on White River NWR, 1993–1995. ($F = 8.01$, $df = 5, 279$ $P < 0.001$; Error bars represent ± S.E.).

for 79% of all predation events, with the largest percentage of nest failures occurring in the egg stage across all types of failures.

DISCUSSION

Information on the nesting biology of the Acadian Flycatcher is scarce, with the previous detailed studies being from the northern periphery of the species' range in Michigan (Mumford 1964, Walkinshaw 1966). Thus, demographic analysis in different geographical regions is warranted. Our data represent the first demographic analyses of Acadian Flycatchers in the Lower Mississippi Alluvial Valley, and the total number of nests investigated (n = 601) was substantially larger than previous studies.

Nesting success.—Nesting success of Acadian Flycatchers on White River NWR varied from 10% to 25% annually (Mayfield estimate) over the three years of the study; the fraction of total nests fledging young varied from 16–30%. These estimates of nesting success are considerably lower than the 64.5%

TABLE 2. Mayfield estimates of nest survival for Acadian Flycatchers at White River NWR, 1993–1995.

	Mean nest survival rates[a]				
			Nesting period		
	Egg stage daily	Nestling stage daily	Daily	29 days[b]	Exposure days[c] (n)
1993	0.920 (0.016)	0.927 (0.024)	0.922 (0.013)	0.10	374.5 (37)
1994	0.953 (0.006)	0.930 (0.010)	0.945 (0.005)	0.18	1534 (128)
Early[d]	0.950 (0.007)	0.915 (0.014)	0.938 (0.007)	0.13	1127 (101)
Late[e]	0.966 (0.011)	0.964 (0.014)	0.965 (0.009)	0.36	407 (27)
1995	0.954 (0.004)	0.953 (0.005)	0.953 (0.003)	0.25	4040 (287)
Early	0.952 (0.005)	0.970 (0.004)	0.960 (0.003)	0.31	3290.5 (196)
Late	0.958 (0.007)	0.948 (0.009)	0.954 (0.005)	0.25	1258 (91)

[a] Mayfield estimates of mean daily nest success for the egg, nestling, and combined nesting period (± 1 SE).
[b] Nest survival for the combined egg (15 days) and nestling period (14 days).
[c] Exposure days are summed over the egg period (from first egg) and nestling period (number of nests).
[d] Nests initiated before 14 June.
[e] Nests initiated on or after 14 June.

TABLE 3. Summary of Acadian Flycatcher nests with known outcomes, White River NWR, 1993–1995.

	Fates[a] (%)			Failures (%)
	1993 (n = 42)	1994 (n = 129)	1995 (n = 306)	1993–1995 (n = 340)
Successful	16.6	29.5	30.0	—
Predation	66.6	56.6	50.6	75.3
Parasitism[b]	12.0	1.5	6.0	7.3
Abandoned	4.8	6.2	9.1	11.2
Weather	—	6.2	1.0	3.2
Inundation	—	—	2.3	2.0
Observer	—	—	1.0	1.0

[a] Excludes nests with unknown outcomes (1993, n = 50; 1994, n = 42; 1995, n = 32).
[b] Failures attributed to brood-parasitism include nests that fledged ≥1 cowbird young but no host young, as well as nests that were abandoned because of parasitism.

and 67.4% (fraction of nests fledging young) reported by Walkinshaw (1966) and Li (1994), respectively. However, Walkinshaw's data are 30 years old and may represent different degrees of forest fragmentation and environmental processes (e.g., nest predation and brood-parasitism) than today. Li (1994) evaluated the nesting success of several migratory bird species in the Ozark National Forest, a large contiguous tract of upland forest in northwestern Arkansas. In comparison, White River NWR, although large, is a long narrow fragment of bottomland forest surrounded by a large expanse of agriculture along the White River.

Estimates of nesting success for 1993 should be interpreted with caution since nests were only monitored during the month of June, reflecting events early in the breeding season. The large difference in estimates of nesting success between 1993 and 1994–1995 demonstrates the need for using caution when using partial data. That is, observed differences in nesting success may not be related to environmental factors but instead to experimental design (e.g., time period studied). For instance, late nests were more successful in 1994 and tended to be more successful in 1995 though not statistically.

Predation.—Nest predation on White River NWR was high, accounting for 75% of all known nest failures. Snakes and avian species were thought to be the leading predators of Acadian Flycatcher nests based on nest appearance at time of failure and anecdotal observations. Failures in which the entire contents of the nest disappeared between checks accounted for 79% of all nest failures. Gray rat snakes (*Elaphe obsoleta spiloides*) were observed depredating three Acadian Flycatcher nests and consumed the entire contents of the nest. Red-bellied Woodpeckers (*Melanerpes carolinus*) were also observed depredating Acadian Flycatcher nests on other bottomland sites in Tennessee (M. Marshall, pers. comm.) and Louisiana (K. Ouchley, pers. comm.), removing the entire nest contents. Barred Owls (*Strix varia*) present in high densities (pers. obs.) may have destroyed nests as suggested by Walkinshaw (1966).

Parasitism and clutch size.—Our data for nonparasitized nests are identical to reported clutch sizes for Acadian Flycatchers of 2.9 (range 2–4, mode = 3, Mumford 1964); 2.9 (range 2–3, mode = 3, Walkinshaw 1966); and 2.9 (Li 1994). Walkinshaw (1966) stated that in Michigan clutch size varied across the breeding season with first clutches being larger than second or replacement clutches. On White River NWR, clutch size also decreased from 2.9 ± 0.02 in early nests to 2.7 ± 0.06 in late season nests.

Cowbird parasitism was low (21% of all nests) compared with parasitism rates of other species in the midwestern United States (Robinson 1992; Robinson et al. 1995a, b), resulting in a small portion (7%) of all nest failures attributable to high rates of nest predation. Walkinshaw (1961) suggested that Acadian Flycatchers discontinue incubation of host eggs when cowbird eggs hatch first, resulting in failure of host eggs to hatch. However, Acadian Flycatchers are capable of producing a successful brood when host eggs hatch first. Of 104 parasitized Acadian Flycatcher nests, 2% were able to successfully produce conspecific young as well as a Brown-headed Cowbird young. In both cases, Acadian Flycatcher young hatched earlier than the cowbird young.

Brood-parasitism also influenced Acadian Flycatcher clutch size across the breeding season (i.e., early and late nests). Parasitized nests had smaller clutches for first nesting attempts and replacement clutches, presumably because cowbirds removed host eggs. However, parasitized nests had larger clutch sizes late in the breeding season, suggesting that cowbirds are not removing host eggs late in the breeding season.

In summary, the population of Acadian Flycatchers in this study appears to be influenced primarily by high rates of nest predation, for brood-parasitism by Brown-headed Cowbirds contributed only a small amount to overall nest failure. However, both factors influenced early nesting attempts more than late nesting attempts. It is not known if birds fledging late in the breeding season have a decreased probability of survival compared with early fledges, but this factor certainly has the potential to influence population dynamics. Other factors that could play critical roles in population dynamics of Acadian Flycatchers in bottomland forests include number of renesting attempts and broods, food abundance, and loss of appropriate habitat features. Consequently, future research with color-banded individuals should focus more on productivity (number of young per pair per year), annual survival of adult and juveniles, and habitat features that influence these parameters.

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